Identifying environmentally-driven spatial clustering in population trends of large gulls in south-west Scotland and Northern Ireland

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Running head: Spatial clustering in gull trends

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Capsule Spatial clustering was observed in colony growth rates of three large UK gull species with proxies of local marine and intertidal resources explaining part of this variation in two species.

Aims To investigate spatial clustering in colony growth rates of three gull species and determine which environmental variables may explain any spatial clustering observed.

Methods Colony growth rates were calculated for Herring Gull *Larus argentatus*, Lesser Black-backed Gull *L. fuscus* and Great Black-backed Gull *L. marinus* to identify spatial synchrony and to relate to proxies of local foraging conditions in coastal habitats.

Results Spatial clustering in growth rates was found in the gull species. Herring Gull colonies located in areas with greater availability of intertidal prey and fishery activity had higher growth rates. Lesser Black-backed Gull colonies in areas of higher chlorophyll a concentrations experienced more negative growth rates suggesting a negative effect in areas of potential local runoff from agriculture and built-up areas.

Conclusion Spatial clustering in the gulls' colony growth rates indicated that local colonies did experience similar environmental conditions; helping identify variables influencing coastal populations of two gull species, highlighting the importance of marine habitats. These results highlight the need for species and area-specific management for these species of conservation concern.

Introduction

Animal population changes vary over time and space, with patterns often differing over different temporal and spatial scales (McArdle *et al.* 1990, Sutherland & Baillie 1992, Brown *et al.* 1995). Variation in population trends can be driven by differences in environmental variables as well as by density-dependent processes, such as competition and predation (Furness & Birkhead 1984, Brown *et al.* 1995, Sibly & Hone 2002, Crespin *et al.* 2006). Often drivers of population changes are identified using long-term data sets from single populations which can compromise the generality of the findings. Alternatively, spatial clustering in population trends between different populations of the same species, or co-occurring populations of different species can provide a 'pseudo-experimental' approach that treats spatial contrasts in population trajectories as 'treatments' (Baum & Worm 2009). This spatial approach can identify factors that correlate with between-population differences (Frederiksen *et al.* 2005, Robinson *et al*. 2013) and help in understanding larger-scale changes in a species' abundance (Liebhold *et al.* 2004).

Differences in environmental variables, particularly climatic conditions and food availability, can drive variation in population trends (Newton, 1998). In recent decades, many ecosystems are also being impacted upon by anthropogenic influences; affecting population sizes through over-exploitation of resources, introduction of invasive species and habitat destruction/modification (Butchart *et al*. 2010). Different environmental variables are likely to impact populations over different spatial scales, from predation and disturbance acting at a local level to severe or unusual weather events which can act over small and larger spatial scales. When spatially distinct populations fluctuate synchronously this may indicate that populations are connected by dispersal or that similar environmental conditions are occurring over the scale being measured (Moran effect), affecting those multiple populations similarly (Harald *et al.* 2002, Liebhold *et al.* 2004). Contrasting abundance trajectories between spatially distinct populations may, conversely, indicate the local environmental conditions that may drive this variation differ between the distinct populations (Ens *et al*. 2009) or that some populations are able to buffer themselves more effectively against adverse conditions (Burger & Piatt 1990). For instance, generalists, which typically consume the most abundant food, may switch to an alternative resource. Spatial clustering in population trends may be more likely in species which are affected by drivers acting over smaller spatial scales and in species which show higher site fidelity (Erwin *et al*. 1981, Parsons *et al.* 2008).

The extent of spatial clustering has important implications for the understanding of changes in abundance across the distribution of a species and their population management. For species that shows spatial clustering in population trends, if this is due to variation in environmental conditions, then there might be multiple drivers of population changes depending on the local environment. Population management strategies, if required, will therefore depend on local environmental conditions. Populations of apex predators, such as seabirds, often depend on conditions at lower trophic levels (Boyd *et al*. 2006, Fossi *et al*. 2012) and if the local environment varies between geographically distinct populations, findings from one population may not necessarily apply to others. Spatial variation in demographic traits have been found to exist in seabird populations across different scales with inter-population differences found in adult survival, productivity and population growth rate (Frederiksen *et al.* 2005, Harris *et al.* 2005, Bertram *et al.* 2015, Cordes *et al.* 2015, Nager & O'Hanlon in press). However, spatial variation in population trends is generally still poorly understood with the extent to which it occurs in populations likely to depend on the species and habitats of interest.

Within the foraging environments used by seabirds coastal habitats are particularly affected by anthropogenic and natural pressures due to their accessibility and location at a boundary between marine and terrestrial ecosystems, resulting in being impacted from both environments (Thompson *et al*. 2002, Lopez y Royo *et al.* 2009). Species utilising this coastal habitat have experienced declines in recent decades (Lotze *et al.* 2006, van Roomen *et al.* 2012). Among seabirds that particularly rely on coastal habitats for foraging, and have experienced recent declines, are the large gulls: Great Black-backed Gull *Larus marinus*, Lesser Black-backed Gull *L. fuscus* and Herring Gull *L. argentatus* (Eaton *et al*. 2015). As gulls are generalist and opportunistic foragers, exploiting both marine and terrestrial resources (Götmark 1984, Pearson 1968), their populations may be affected by the environment at both sides of the boundary between land and sea. However, the three large gull species differ in their traditional foraging habits. Herring Gulls mostly rely on intertidal foraging habitats whereas Lesser and especially Great Black-backed Gulls scavenge on fishery discards to a greater extent than Herring Gulls; whilst Lesser Black-backed Gulls also forage more frequently inland on farmland, built-up areas and landfill sites (Hunt 1972, Kubetzki & Garthe 2003, McLellan & Shutler 2009). If food resources from their traditional marine intertidal and offshore habitats provide higher quality resources than terrestrial-

anthropogenic habitats (Pierotti & Annett 1991, Annett & Pierotti 1999) then we expect a predominant influence of these habitats on population changes. Alternatively, if terrestrial anthropogenic habitats provide more predictable and abundant food (Burger & Gochfeld 1983, Horton *et al*. 1983), even if of potentially lower quality, these alternative foraging habitats may buffer populations against poor availability of their traditional marine food resources.

This study focuses on the coastal habitats of a region in north-west Europe which has experienced particularly high levels of anthropogenic pressure (Halpern *et al*. 2008). Here we aim to determine whether spatial clustering occurs in the population trends of the three large gull species within a region that shows variation in the coastal habitat that the gulls depend on for breeding and foraging. Where spatial clustering occurs we will explore whether local environmental variables reflecting terrestrial anthropogenic (area of farmland and built-up land, number of landfill sites) and traditional marine food resources (quality of intertidal habitat, fish abundance, marine productivity) might explain between-colony differences in population trends; and whether terrestrial anthropogenic resources, where present, can buffer for poor availability of traditional marine food resources. As the three study species differ in their foraging ecologies we expect each species to be affected by different environmental variables. We will also explore whether colony trends are affected by intra-specific competition for limited resources. This study can provide insights into potential drivers of population trends in the larger gulls that can inform management decision for these species of current conservation concern.

Materials and methods

Study region and study species

The study region incorporates an area of south-west Scotland and Northern Ireland covering two biogeographically distinct regional seas (the north Irish Sea and the south Minches and West Scotland Sea; JNCC 2014), within an area of approximately 200 by 250 km (Fig. 1), providing variation in environmental conditions within a relatively small geographic area. At this regional scale it is known that the three large gull species have experienced contrasting population changes, both between and within species (Mitchell *et al*. 2004, Nager &

O'Hanlon in press); therefore providing a suitable region to investigate spatial clustering in gull population abundance at the colony level.

It is uncommon to have simultaneous colony counts from multiple colonies over a larger geographical area. No regular counts exist for the gull colonies in the study region, therefore the seabird censuses of the UK and Ireland (Mitchell *et al*. 2004) provides a rare opportunity to investigate multiple colonies within a larger area. Breeding Herring, Lesser Black-backed and Great Black-backed Gulls within this region were counted as part of three national censuses across the UK and Ireland between 1969 and 2002: Operation Seafarer in 1969 (Cramp *et al*. 1974), Seabird Colony Register in 1985-1989 (Lloyd *et al*. 1991), and Seabird 2000 in 1998-2002 (Mitchell *et al*. 2004). All three censuses had complete coverage of the region and for each of the selected species used the same survey methodologies (Mitchell *et al*. 2004). We used the adjusted counts of Apparently Occupied Nests (AON) per colony from the Seabird Monitoring Programme (Walsh *et al.* 1995, JNCC 2012) and additional data for Operation Seafarer from JNCC (Roddy Mavor, pers. comm.). Only coastal colonies within 5 km of the coast were included as we were interested in the interface between marine and terrestrial coastal habitats. Although the temporal resolution with three censuses over three decades is relatively low, changes in colony size were consistent between the censuses for two of the three gull species (see results).

Spatial variation in colony growth rates

To estimate long-term population trends for each of the three gull species we extracted species-specific counts of individual breeding colonies from the three national seabird censuses. During the seabird censuses grid references of all counted colonies were recorded. We matched counts from the same colony in different censuses by importing the grid references into ArcGIS (ArcMap ver.10. ESRI, USA) and extracted the location of all counts. Only where locations between censuses matched, by name or grid reference within 500m, we assumed successive counts for the same colony. For small islands and sea-lochs (less than 5 km^2 in area), where the level of sub-sites counted was different between censuses, we totalled all counts within such sites into one value so that total counts were comparable between censuses.

Over the three census periods some colonies were newly established whilst others went extinct, which could be identified if their absence (a count of zero) was recorded.

However, where no record of a zero count was made we could not be certain that the colony had been monitored within that census, therefore these colonies were not included in the analysis. The number of colonies with no information was largest in the Seabird Colony Registry and therefore, in the analysis we only included colonies that reported a count, including a zero count, in Operation Seafarer (1969-1970) and in Seabird 2000 (1998-2002). This ensured that colony growth was estimated for all colonies over the same period of time, and therefore were comparable, and maximised our sample sizes. The total number of individual colonies for each species within the study region, for which data was available in the first and last census, are displayed in Table 1.

The conventional calculation of growth rate lambda, (N_{t+1}/N_t), is not defined for newly established colonies. We therefore calculated colony growth rates (GR) for individual colonies using a formula based on Guillaumet *et al*. (2013):

$$GR = (N_t - N_{t-1})/\text{Maximum } [N_t, N_{t-1}]$$

where N_t is the count in Seabird 2000, N_{t-1} the count in Operation Seafarer, and Maximum $[N_t, N_{t-1}]$ is the highest count from either Operation Seafarer or Seabird 2000. This calculation of GR avoids the issue of undefined growth rate for newly established colonies and GR = 0 for extinct colonies (Guillaumet *et al*. 2013), both of which occurred at the colony level. GR values were monotonically related to the calculated lambda with $r_s = 1.0$ in all species.

Environmental correlates of colony growth rates

Where spatial synchrony in population changes occurred, we also wanted to identify any environmental factors, reflecting availability of resources used by gulls, that might explain inter-colony variation. As all three large gull species are generalist foragers (Pearson 1968; Götmark 1984, Camphuysen 1995), we selected environmental factors that covered the range of known resource use of the gulls: marine invertebrates in intertidal habitats; fish in offshore marine habitats and farmland and anthropogenic food sources in the terrestrial habitats.

An important foraging habitat for large gulls, and in particular for Herring Gulls, is the intertidal zone where they forage on a large diversity of invertebrate prey (Götmark 1984). We extracted information both on the area of intertidal habitat and the average wave fetch as a proxy for food availability in the intertidal zone. The area of intertidal habitat was obtained from Landcover 2000, which uses computer classification of satellite images to

quantify different land uses in the UK (Fuller et al. 2002). Wave fetch, a measure of the exposure of the coastline that depends on topography, was included as a proxy for potential intertidal foraging habitat quality. For rocky shoreline, which is the predominant coastal habitat in the study region, low wave fetch supports a greater abundance and diversity of potential intertidal prey species (Burrows *et al*. 2012). Wave fetch was available for quadrats of 200m^2 along the coastline by Burrows (2009).

All three species also forage out at sea, with Lesser and Great Black-backed Gulls to a greater extent than Herring Gulls, where they can feed on small pelagic fish but mainly scavenge on fishing discards (Spaans 1971, Camphuysen 1995, Tasker *et al.* 2000, Kubetzki & Garthe 2003, Tyson *et al.* 2015). To characterise local marine foraging habitats we included sea surface temperature (SST), chlorophyll a concentration and fishery data. SST (11µ night-time) and chlorophyll a concentration (mg/m^3) were included as proxies for primary productivity in the marine environment. SST influences marine processes associated with thermoclines and upwelling which will affect the distribution and abundance of potential prey species, whilst chlorophyll a concentration acts as a proxy for primary productivity at the base of marine food webs (Huot *et al*. 2007). We extracted summer seasonal composites of SST and chlorophyll a concentration for 2002, to relate to marine productivity during the breeding season, from Aqua MODIS at 4 km resolution (http://oceancolor.gsfc.nasa.gov/cgi/l3). For the UK there are no publically available data on discard tonnages (Gibson *et al.* 2015) and landing data are only available on a coarser spatial level than we use here. Instead we assumed that fishery activity is greater where fish are more abundant and therefore extracted demersal fish abundance from the International Bottom Trawl Survey (IBTS) data at the ICES (International Council for the Exploration of the Sea) sea area level (Fig. 1; data obtained from https://datras.ices.dk/Home/Descriptions.aspx). Our study region encompassed four of these sea areas and for each we averaged the total catch per unit effort (CPUE) of all fish age classes trawled during the spring survey (Quarter 1) for 1998-2002.

Gulls also exploit resources from terrestrial habitats by foraging on fields, where they take earthworms and grain, and by scavenging on landfill sites and other built-up areas such as in coastal towns (Pons 1992, Belant *et al*. 1993, Coulson & Coulson 2008). We therefore extracted farmland and built-up areas from Landcover 2000 (Fuller *et al*. 2002). Built-up area is defined as the area covered by buildings and gardens in suburban/rural developed areas and

continuous urban areas. Farmland was categorised as the area covered by agriculture and improved grassland. The number of landfill sites for Scotland was obtained from the Scottish Environment Protection Agency (SEPA, 2015) and for Northern Ireland from the Northern Ireland Environment Agency (NIEA, Eugene Kelly, pers. comm.).

Each environmental variable was extracted from within the gulls' potential foraging range around each of the colonies. The average maximum foraging distance from the colony for breeding Herring Gulls is estimated at 50 km (Pearson 1968, Götmark 1984, Camphuysen 1995, Thaxter *et al.* 2012). We also observed foraging trips of up to 40 km from the colony for a small subsample of Herring Gulls in our study region. As all three species can access resources as far as 50 km considering smaller foraging ranges would therefore likely ignore resources potentially available to the birds. Lesser and Great Black-backed Gulls can have larger average maximum foraging ranges, especially foraging further offshore than Herring Gulls (Camphuysen 1995, Thaxter *et al.* 2012). Therefore, for colonies that were less than 50 km from the boundary between two ICES sea areas we selected the higher CPUE value of the two ICES sea areas within their foraging range. Spatially-explicit environmental data for the whole study region are difficult to obtain, and are generally only available for the more recent years. We could only extract static environmental data for the end of the census period rather than extracting information on the change in these variables over time, therefore we investigated potential drivers of the spatial variation in colony GR at the end of the census period.

Data on proxies for the gulls' resource availability may have changed over the seabird census period; however spatially-explicit data was only available at the end of this period. We cannot therefore determine directly what the drivers of spatial clustering in colony GR within the region were. However, they can still be informative when investigating spatial clustering in colony trends at the end of the census period. The amount of farmland and built-up area and number of landfill sites, as a proxy for terrestrial anthropogenic food availability are based on information from 2000, at the end of the period of interest. Although the absolute values of these variables have likely changed over time levels relative to each other are thought to have remained largely the same, with areas with the greatest human impact in the late 1960s also being the areas with the greatest human impact in 2000. Although Landcover data was available for 1990 (Fuller *et al.* 1994) it could not be included in the analysis as it did not cover Northern Ireland. However, for Scotland, there was a

significant positive correlation between the amount of built-up area around the gull colonies during 1990 to that in 2000 ($r_{149} = 0.87$, $P < 0.001$). Data for SST and chlorophyll a concentration was also only available for the end of the census period, extracted for 2002 as this was the earliest data was available for at the required resolution. The values of these two variables will also vary annually, however we are more interested in the relative spatial variation in marine productivity rather than absolute values; with relative values for SST and chlorophyll a concentration in the following ten years similar across the region.

Statistical analysis

All statistical analyses were performed in R, Version 3.1.1 (R Development Core Team 2015). To investigate spatial clustering in colony GR on an objective basis we used spatial autocorrelation analyses. For each species we calculated a Moran's *I* Index using the *lctools* package in R (Paradis *et al*. 2004). Moran's *I* Index is a measure of spatial autocorrelation, based on each species' colony GR and the colony's latitude and longitude. Moran's *I* Index ranges from -1 (spatially dispersed, where neighbouring colonies have different values of GR) to +1 (spatially clustered, where neighbouring colonies have similar values of GR) (Moran 1950, 1953, Legendre & Fortin 1989). A *I* value of zero indicates a random spatial pattern of GR. To statistically test whether Moran's *I* Index differs from 0 it can be transformed to *Z*-scores with values greater than 1.96 indicating *I* is significantly greater than 0 (spatially clustered) or smaller than −1.96 then indicating *I* is significantly less than 0 (spatially dispersed), indicating significant spatial autocorrelations at $P < 0.05$. To visualise the spatial clustering of the three gull species we carried out K-means clustering (MacQueen 1967) using the kmeans function from the *stats* package in R. To identify the most appropriate number of clusters, k, the elbow criterion was used which considers the amount of variance explained by different number of clusters based on a plot of the within group sums of squares. To visualise the spatial variation in colony GR across the study region for each species the locations of colonies were plotted in ArcMap 10.1 and shaded based on the GR clusters.

To test which characteristics of the coastal environment were related to within-species variation in colony GR we used general linear models with colony GR as the response variable and environmental variables (SST, chlorophyll a, CPUE, wave fetch, built-up area, farmland and number of landfill sites) as explanatory variables. As the effect of environment

conditions on colony GR may depend on the number of individuals competing for that resource, we also included colony size and its interaction with the environmental variables in the model. We used colony size from Seabird 2000 to match the time frame environmental information was available, as we were investigating the structure at the end of the census period for when spatially-explicit environmental information available. We tested for multicollinerity between explanatory variable in the *car* package (Fox & Weisberg 2011) removing variables with a Variance Inflation Factor (VIF) greater than three (Zuur *et al*. 2010). This resulted in the number of landfill sites being removed from all statistical models; chlorophyll a concentration being removed from the Herring Gull and Great Black-backed Gull models; and built-up area being removed from the Lesser Black-backed Gull model.

Starting with the most complex model, including biologically relevant second-order interactions, backwards stepwise model selection, to establish the minimal adequate model, was carried out using Likelihood Ratio tests to determine whether the exclusion of a term resulted in a significantly poorer fit of the model (Crawley, 2007). Significance thresholds were set at $P < 0.05$, and only significant interaction terms are shown. Residual plots were inspected to ensure no deviations from homoscedasticity or normality occurred, and if necessary data were transformed (colony size was natural logarithm transformed).

RESULTS

Population growth rates

Between the first and last national seabird census the abundance of all three large gull species declined (Table 1); although this was only significant for the Herring Gull ($t_{67} = 2.53$, $P = 0.014$). For the analysis we assumed that colony GR across the census period was monotonic (annual counts for the included colonies were not available over this period); the most recent population change (GR between 1985-2000 available for a subset of colonies) was correlated with the change over the whole census period (1970-2000) for Herring Gulls ($r_{49} = 0.62$, $P < 0.001$) and Great Black-backed Gulls ($r_{31} = 0.79$, $P < 0.001$), but not for Lesser Black-backed Gulls ($r_{20} = 0.33$, $P = 0.126$). Therefore, when investigating which environmental variables could explain spatial variation in the colony GR of Lesser Black-backed Gulls across the region colony GR from the reduced sample of 21 colonies between the second (1985-1989) and last (1998-2002) censuses were instead included as the response variable.

In all three species we found a statistically significant spatial clustering of colony GR over the entire census period across the study region (Table 1). Colonies of all species generally increased around the Firth of Clyde with declines around the northern Solway Firth. Both Herring and Great Black-backed Gulls declined across Northern Ireland to a greater extent than the Lesser Black-backed Gull, whereas the trends for colonies in the Southern Hebrides were more variable between the species (Figure 2). Herring and Great Black-backed Gull, but not Lesser Black-backed Gull, colonies mainly declined in their former strongholds; we found negative effects of colony size in 1969-1971 on the colony GR between 1969-1971 and 1998-2002 from linear regressions: Herring Gull: $F_{1,66} = 16.85$, $P < 0.001$; Great Black-backed Gull: $F_{1,46} = 10.34$, $P = 0.002$; Lesser Black-backed Gull: $F_{1,31} = 2.73$, $P = 0.109$.

Environmental correlates of population growth rates

Different proxies of local food availability within the colony's foraging range were found to explain part of the spatial variation in colony GR for the three gull species. In Herring Gulls (Table 2b) there was a significant, negative relationship of colony GR with average local wave fetch (Fig. 3a); and significant positive relationships with CPUE (Fig. 3b) and SST (Fig. 3c). Herring Gull colonies with increasing GR were recorded in more sheltered locations with lower wave fetch and in areas where the CPUE of benthic fish were higher. In addition, colony declines were greater at locations with lower mean SST within the foraging range of the colony. In Lesser Black-backed Gulls colony GR was negatively correlated with chlorophyll a concentration (Table 2c); with colonies declining to a greater extent in areas of higher mean chlorophyll a concentration within the colony's foraging range (Fig. 4). In Herring and Great Black-backed Gull, but not in Lesser Black-backed Gulls, colonies which experienced the highest GR also had the largest colony counts in Seabird 2000. However, colony size did not interact with any of the environmental variables suggesting no evidence for limited resources in any of the species (Table 2).

DISCUSSION

We found evidence for spatial clustering of colonies of two of the three gull species with respect to colony GR across south-west Scotland and Northern Ireland; for Great Black-backed and Herring Gulls, however the pattern was not statistically significant for Lesser Black-backed Gulls. This spatial clustering suggests that over the census period gull colonies

in close proximity were likely to experience similar environmental conditions which influenced their colony GR. We also identified environmental variables that were related to the spatial clustering for Herring Gulls: colonies had higher growth rates when located in areas with more sheltered coasts; near areas where there was potentially a greater abundance of demersal fish and in areas where average local SST was higher. For the Lesser Black-backed Gulls, colonies had higher growth rates in areas of lower chlorophyll a concentrations in the marine environment. None of the environmental variables we included were associated with variation in Great black-Backed Gull colony GR. These results suggest that relatively small scale variation in environmental conditions can affect changes in population abundance in gulls and that the different species are affected by different drivers.

We found spatial variation in colony growth for all three gull species on a relatively small spatial scale, with clustering based on the direction and extent of individual colony GR, and this pattern was statistically significant in the Herring and Great Black-backed Gull. There were both similarities and differences between the spatial clustering of the Great Black-backed, Herring and Lesser Black-backed Gulls. Spatial synchrony in population trends has been observed in other seabird species, and over larger spatial scales (Frederiksen *et al.* 2005, Cook & Robinson 2010, Bertram *et al.* 2015); and in the large gull species on the scale of the British Isles (Nager & O'Hanlon in press) indicating that nearby seabird colonies may frequently be influenced similarly by what is occuring in the local environment. This has implactions for conservation stratergies for these speices of conservation concern as one common stratergy across a large geographic scale is unlikely to be effective for all populations.

Geographic variation in colony growth, as found in the three gull species, could be due to spatial variation in deterministic processes, such as strength of density dependence, and/or due to spatial variation in environmental conditions (Moran effect) (Brown *et al.* 1995, Williams *et al.* 2003, Liebhold *et al.* 2004). We found a significant negative relationship between colony growth and the size of the colony at the start of the census period for the Herring and Great Black-backed Gulls indicating that the colonies which declined the most over the census period were those that were the largest during the first census. Evidence for density-dependent population changes have also been found at the national level in the Herring Gull and the Lesser Black-backed Gull (Nager & O'Hanlon in press). Larger colonies may deplete local food sources more strongly and experience higher levels of

403 competition resulting in reduced colony growth (e.g. Furness & Birkhead 1984, Birt *et al.*
404 1987, Lewis *et al.* 2001). It would be expected that such processes would be indicated by
405 interactive effects of colony size and environmental conditions on colony growth, however
406 we did not find evidence in support of this. Deterministic processes are therefore unlikely to
407 explain the observed spatial clustering in colony trends of the large gull species. Instead,
408 spatially variable environmental conditions may be responsible for the geographic differences
409 in colony trends of the gulls.
410
411 Environmental variables acting as proxies of resource availability associated with
412 marine, intertidal and terrestrial habitats, explained part of the variation in colony GR of
413 Herring and Lesser Black-backed Gulls. In Herring Gulls, colonies that were associated with
414 lower average wave fetch in their foraging range had higher colony GR. Wave fetch predicts
415 the composition of rocky shore communities due to the influence of wave exposure on these
416 communities (Burrows *et al.* 2008). Low wave fetch reflects a more sheltered intertidal
417 habitat that generally supports a greater abundance and diversity of intertidal prey species on
418 which the gulls forage (Burrows *et al.* 2008, Burrows 2012). Herring Gulls forage more
419 extensively within intertidal habitats than the other two gull species (Hunt & Hunt 1973,
420 Kubetzki & Garthe 2003) and therefore colonies close to sheltered intertidal habitats may
421 experience higher potential local food availability which results in higher colony GR. In
422 addition, Herring Gulls on more sheltered shorelines may breed more successfully possibly
423 due to these colonies being more sheltered from adverse weather events which could impact
424 upon egg and chick survival or affect the gulls foraging ability (Schreiber 2001). In Herring
425 Gulls increasing colonies were also located within sea areas of higher demersal fish
426 abundance. Higher abundance of demersal fish may mean higher fishery activity and
427 therefore more opportunities to scavenge on discards; a higher quality resource than what the
428 gulls are likely to consume in terrestrial habitats (Hüppop & Wurm 2000, Oro *et al*. 1996).
429 This was with the exception of ICES area 47 where the CPUE was relatively high but the
430 colonies located within this area had experienced large declines. One potential explanation is
431 that this ICES sea area covers a larger area, incorporating areas for away from those occupied
432 by Herring gulls and therefore may not be representative of the potential food availability
433 accessible to them. Both Great and Lesser Black-backed Gulls scavenge more intensively on
434 discards than Herring Gulls (McLellan & Shutler 2009, Ramírez *et al*. 2015, Tyson *et al*.
435 2015, Washburn *et al*. 2013) and therefore we expected that the colony GR of these species
436 would also relate to CPUE. However, this was not found to be the case potentially due to the

coarse resolution of CPUE we included. In addition, within the study region greater numbers of Herring Gulls were found associated with fishing boats, potentially due to the higher numbers of this species in the regions (Furness *et al.* 1988).

In Herring and Lesser Black-backed Gulls, colony GR were associated with measure of marine productivity, however in both cases the relationships were opposite to what we would expect. Typically, higher chlorophyll a concentrations and lower SST reflect high marine productivity; with higher chlorophyll a concentration relates to more productive marine waters (Huot *et al.* 2007), resulting in potentially higher availability of marine prey (Bustamante *et al.* 1995). Whilst, lower SST is typically related to higher marine productivity associated with the timing of thermal stratification and spring blooms (Townsend *et al.* 1994). In Lesser Black-backed Gull colonies one possible explanation for the opposite pattern observed could be attributed to nutrient runoff into coastal waters and sea-lochs masking actual chlorophyll a concentration, as the satellite data cannot distinguish between chlorophyll from phytoplankton and nutrient runoff (Smith *et al.* 1998, Nielsen *et al.* 2002). If this high chlorophyll a concentration does reflect high runoff from local agriculture as well as domestic and industrial waste (Grantham & Tett 1993) this may lead to a decline in benthic marine prey (Hiscock *et al.* 2004, Burrows *et al.* 2008). The model did not include any terrestrial anthropogenic habitats therefore the effect of chlorophyll a concentration on colony GR could also possibly reflect proximity to built-up areas. The observed pattern in the Herring Gull is more difficult to explain. If higher SST in certain locations are attributed to runoff, rather than reflecting natural marine productivity, then, unlike the Lesser Black-backed Gulls, Herring Gulls may benefit from runoff entering coastal waters. As higher nutrient levels can potentially benefit the abundance of some marine invertebrate species, such as starfish (Brodie *et al.* 2005, Chiu *et al.* 2008), which Herring Gulls forage on.

Therefore, for the Herring Gull increasing colonies were located in areas with access to marine resources in terms of potential discards and intertidal prey; and declined in areas where the availability of these resources were lower. This may suggest that Herring Gulls do benefit from having high quality marine resources within the vicinity of the breeding colony (Annett & Pierotti 1999, Blight *et al.* 2015) potentially buffering them from other impacts in the local environment. This may also be the case for the Lesser Black-backed Gull, with areas away from potential high runoff, having between foraging conditions.

In colonies in close proximity to built-up areas it may also have been expected that the presence of potential terrestrial anthropogenic food sources such as landfill sites may benefit the gulls resulting in more favourable colony growth rates. Anthropogenic resources, especially in relation to the vicinity of landfill sites are known to benefit opportunist gulls species in terms of colony size, breeding traits and body conditions (Pons 1992, Duhem *et al.* 2008, Weiser & Powell 2010, Steigerwald *et al.* 2015). Despite these resources generally being thought of as lower quality to the gulls than marine resources (Pierotti & Annett 1991, Annett & Pierotti 1999), they can potentially provide a predictable and abundant food source (Burger & Gochfeld 1983, Horton *et al.* 1983). However, we found no relationship between colony GR and potential terrestrial resources within the vicinity of the colonies o Herring and Great Black-backed Gulls. The negative relationship between the Lesser Black-backed Gull colony GR and chlorophyll a concentration may however potentially indicate that colonies with a high amount of built-up area within the colony range may negatively impact upon this species through runoffs entering the local marine environment; although potentially not for the Herring Gull. This suggests that the two gull species may respond differently to local marine conditions at least in terms of runoff into coastal habitats.

Not all monitored colonies within the study region were included in the analysis due to incomplete records of colony counts; which could be due to the colony not being counted or not being in existence at the time. However, it is thought that the selected colonies do reflect the regional population trends (unpubl. data). For this analysis we selected the average maximum foraging range taken from values in the literature, as well as unpublished tracking data of Herring Gulls from the study region. This means that the average maximum of foraging range of 50km results in the foraging ranges of neighbouring colonies to overlap. However, studies on other seabird species have found that neighbouring colonies do not overlap in their forging areas (Wanless & Harris 1993, Wakefield *et al.* 2013 but see Ainley *et al.* 2004, Evans *et al.* 2015). In addition, foraging ranges are likely to vary with colony size (Jovani *et al.* 2015); with individuals from larger colonies potentially travelling further due to competition and local food depletion in the vicinity of the colony (Furness & Birkhead 1984). It is therefore difficult to accurately estimate the foraging range for every colony however, selecting the maximum foraging distance of breeding gulls will account for all resources that are potentially accessible around the colony.

In opportunistic and generalist species, such as the gulls, the resources most widely available within the foraging range of the colony will likely be the most consumed (Osterblom et al., 2008, White, 2008). The results from this study suggests that when the resources in the vicinity of Herring Gull and Lesser Black Back Gull colonies are from marine and intertidal habitats their GR is more favourable than those which have more terrestrial resources available. This highlights the importance of an intact marine coastal environment to these two species; and especially for the Herring Gull the importance of the intertidal habitat.

We found spatial clustering in at least two of the three large gull species within a relatively small region of 200 by 200km. The results suggest that colony growth rates of Herring and Lesser Black-backed Gulls are sensitive to spatially variable environmental conditions at the interface of marine and terrestrial ecosystems. Identifying the environmental drivers of population changes is challenging and the spatial clustering indicates that these drivers may vary even on a small spatial scale. This study demonstrates that investigating spatial variation in colony growth is a promising approach and highlights the potential of monitoring multiple colonies and identifying spatial variation in population trajectories to help investigate relevant environmental variables that might explain spatial differences in population changes. It also warns that common conservation management might not be equally effective at all sites and highlights the need for area-specific conservation measures.

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Table 1. Moran's *I* Index (measure of spatial autocorrelation) to determine the extent of spatial variation in colony population growth rates (GR ± standard error SE) for seven coastal seabird species. Moran's *I* index values range from +1 (clustered) to -1 (dispersed) with values close to 0 indicating a random pattern.

Species	GR ± SE	N[a]	Moran's *I*	*Z* value	*P* value
Great Black-backed Gull	-0.098±0.09	48	0.458	2.618	**0.009**
Herring Gull	-0.228±0.09	68	0.410	2.740	**0.007**
Lesser Black-backed Gull	-0.032±0.14	33	0.370	1.830	**0.067**

[a]N relates to number of individual colonies included within the analysis with population counts, including counts of zero, in Operation Seafarer (1969-1970) and Seabird 2000 (1998-2002).

Table 2. Final models from general linear regression models relating colony GR to environmental variables and colony size (log transformed) in Seabird 2000 for (a) Great Black-backed Gull (n = 48), (b) Herring Gull (n = 68) and (c) Lesser Black-backed Gull (n=21).

Species	Coefficients	Estimate	Std. Error	*t*	*P*	R^2
(a) Great Black-backed Gull	Intercept	-0.3639	0.0847	-4.298	**<0.001**	
	Colony Size	0.2098	0.0355	5.908	**<0.001**	0.42
(b) Herring Gull	Intercept	-7.9414	2.9615	-2.682	**0.009**	
	Wave fetch[a] (km)	-0.0008	0.0002	-3.837	**<0.001**	
	SST[b] (°C)	0.5759	0.2256	2.553	**0.013**	
	CPUE[c]	0.0003	0.0001	2.200	**0.032**	
	Colony Size	0.1291	0.0244	5.296	**<0.001**	0.50
(c) Lesser Black-backed Gull	Intercept	0.2744	0.1939	1.415	0.173	
	Chl. A (mg/m^3)[d]	-0.0533	0.0234	-2.280	**0.034**	0.17

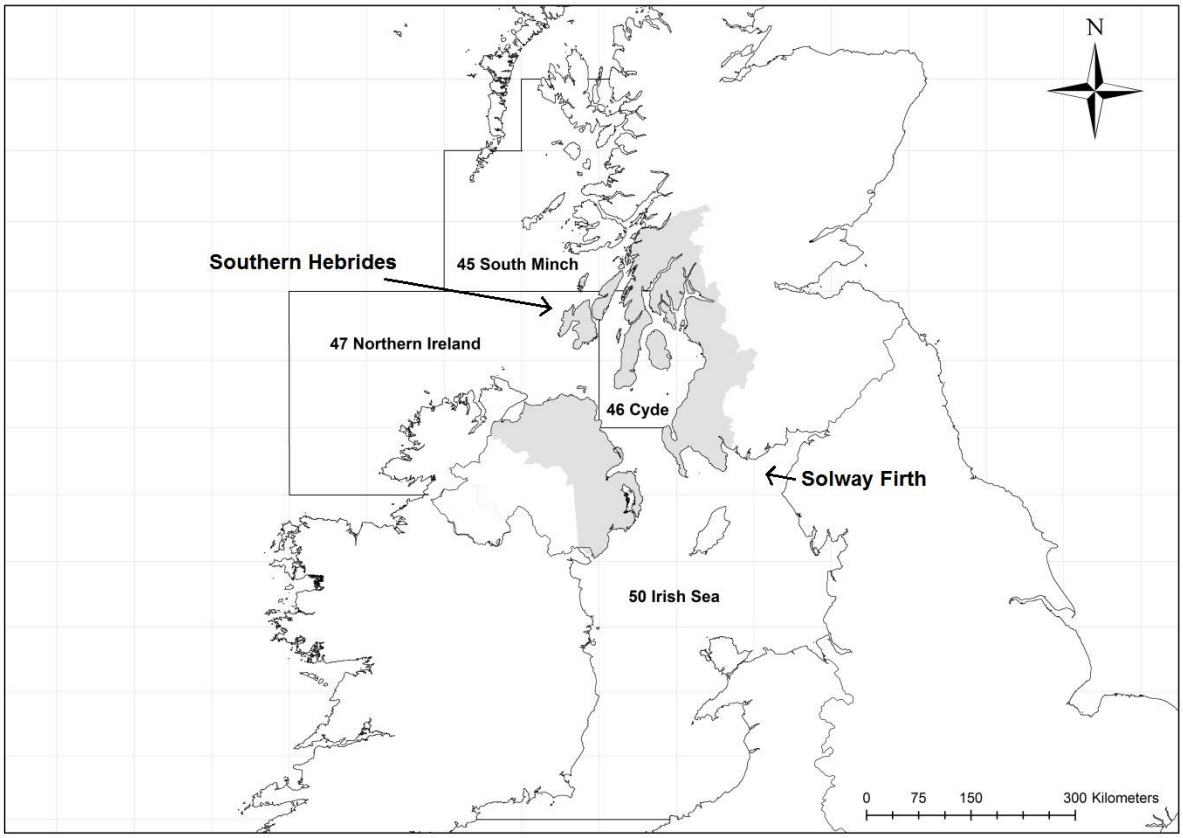
Models started with all variables including interactions between each environmental variable and colony size. [a]Mean wave fetch within 50km of the colony. [b]Mean sea surface temperature (SST) within 50km of the colony. [c]Catch per unit effort (CPUE) during the spring (quarter 1) from International Bottom Trawl Surveys per ICES sea area. [d]Mean chlorophyll a concentration (mg/m^3) within 50km of the colony. The following environmental variables were removed from model (a) Wave fetch $P = 0.96$, CPUE $P = 0.61$, Chlorophyll a $P = 0.44$, Farmland $P = 0.23$, Built-up area $P = 0.12$; model (b) Farmland $P = 0.86$, Chlorophyll a $P = 0.71$, Built-up area $P = 0.11$ and model (c) SST $P = 0.92$, Wave fetch $P = 0.91$, Built-up $P = 0.84$, CPUE $P = 0.66$. Colony GR was calculated for the period between 1969-1970 and 1998-2002 except for the Lesser Black-backed Gull where we took GR between 1985-1989 and 1998-2002 (see text).

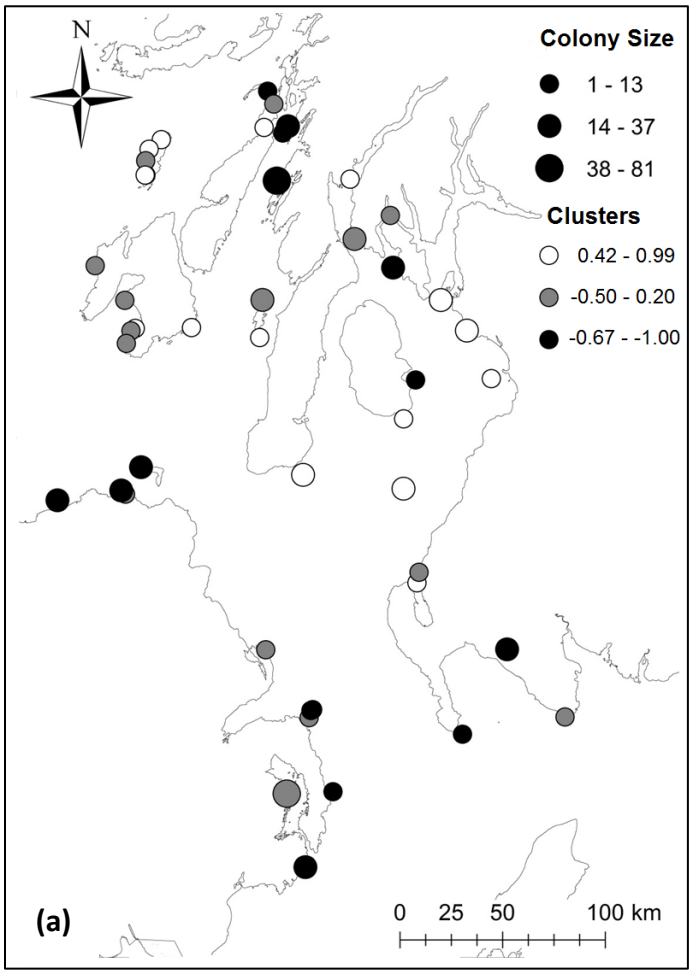
Figure 1. Study region (in grey) where spatial clustering in population trends were assessed for the three large gull species between 1969 and 2002. The study region spanned two Regional Seas: Minches and West Scotland (including ICES sea areas 45, 46 and 47) in the North and Irish Sea (ICES sea area 50) in the South.

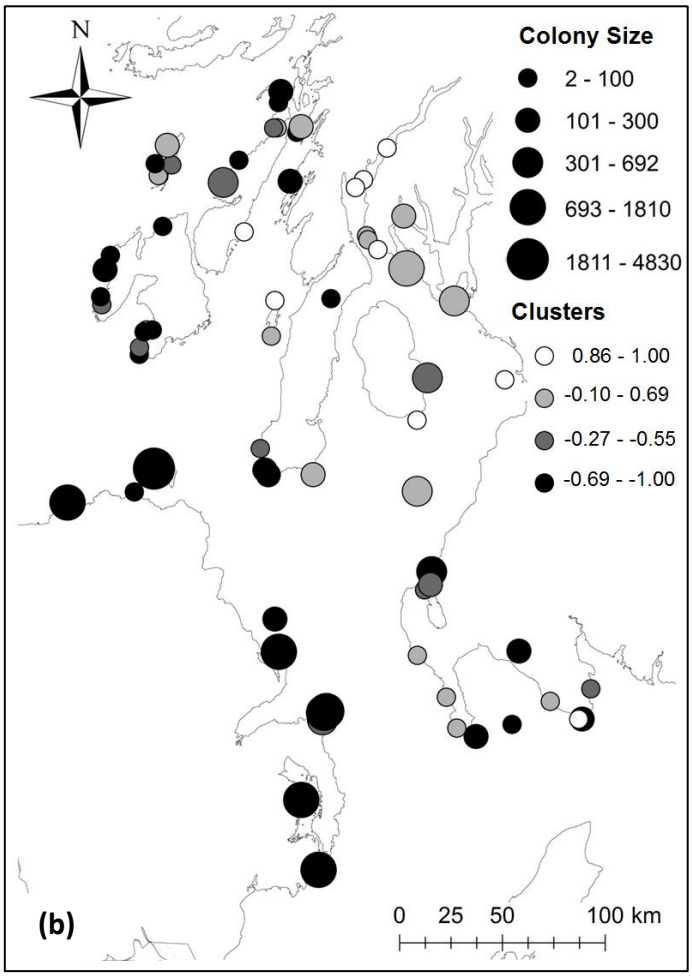
Figure 2. Locations of colonies with sufficient count information (see text) included in the spatial autocorrelation analysis across the study region for (a) Great Black-backed Gull, (b) Herring Gull and (c) Lesser Black-backed Gull. The shade of the circle depicts the extent of colony growth rate between 1969-1970 and 1998-2002; along a gradient of white (strongest increase) to black (strongest decline); categories based on a kmeans cluster analysis (see text). The size of the circle reflects the size of the colony during the first Seabird census, 1969-1970 (separate scales for each species).

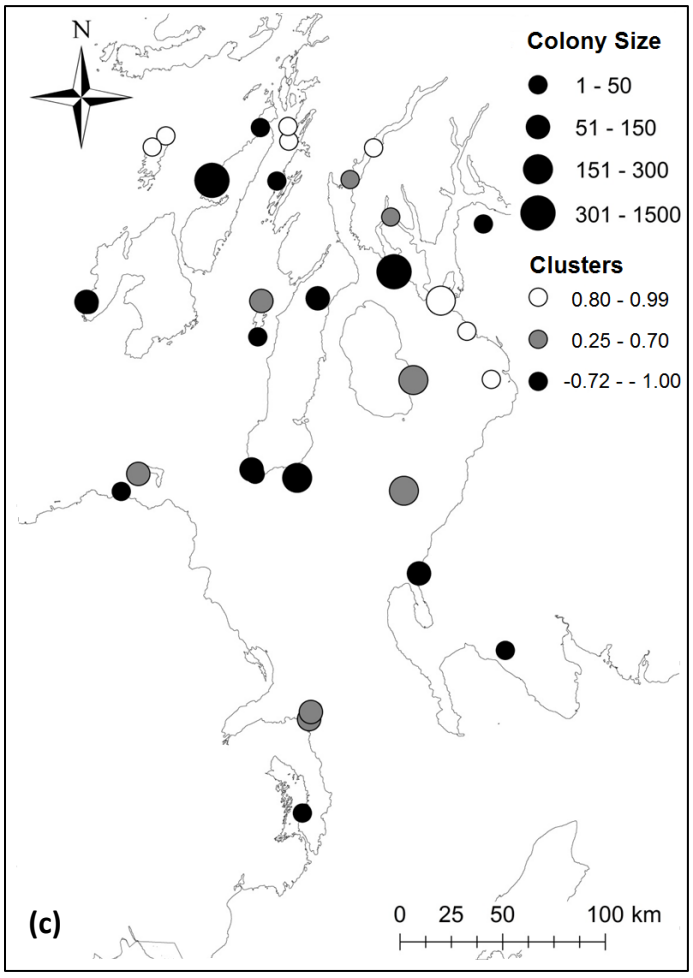
Figure 3. Relationship between Herring Gull colony growth rate, between 1969-1970 and 1998-2002, and (a) average wave fetch (km) within the foraging range of the colony, (b) bottom trawler survey CPUE (catch per unit effort) per ICES sea area and (c) mean sea surface temperature (SST °C) within 50km of the colony (km^2). Data are binned for categories of 200 km wave fetch and per ICES area for CPUE for illustration only. Solid line indicates the trend line with 95% confidence intervals (dashed lines) predicted from a Linear Model.

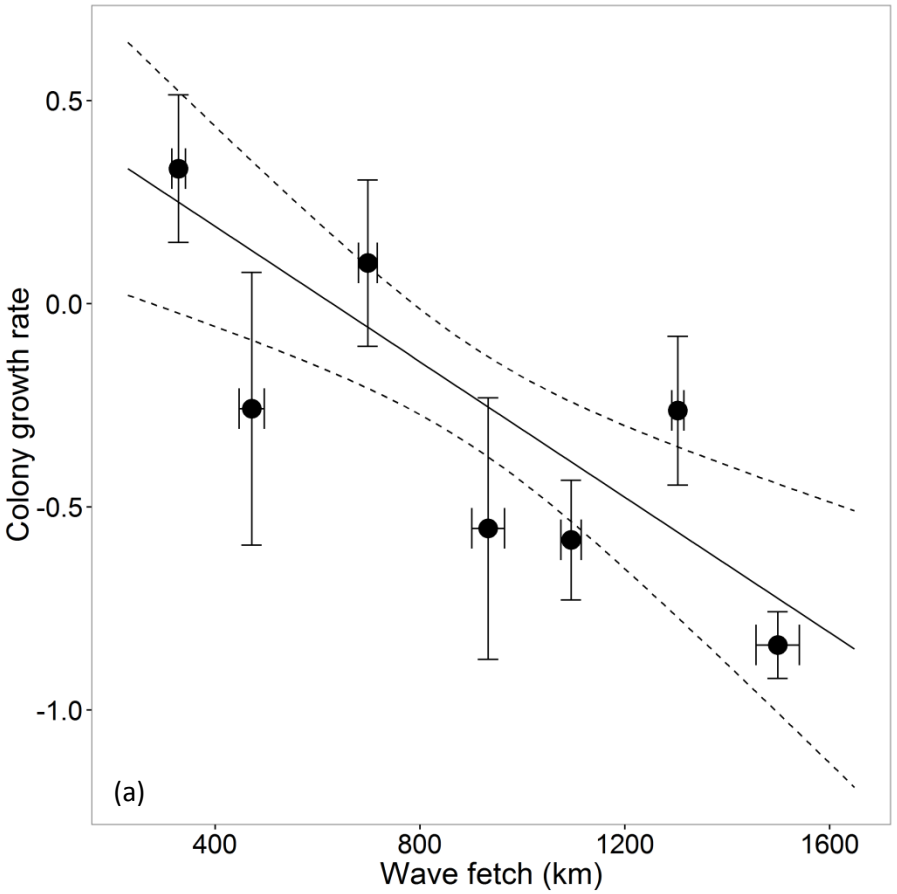
Figure 4. Relationship between Lesser Black-backed Gull colony growth rate, between 1985-1989 and 1998-2002, and mean chlorophyll a concentration (mg/m^3) within 50km of the colony (km^2). Data are binned for categories of 2.5 mg/m^3 chlorophyll a concentration for illustration only. Solid line indicates the trend line with 95% confidence intervals (dashed lines) predicted from a Linear Model.

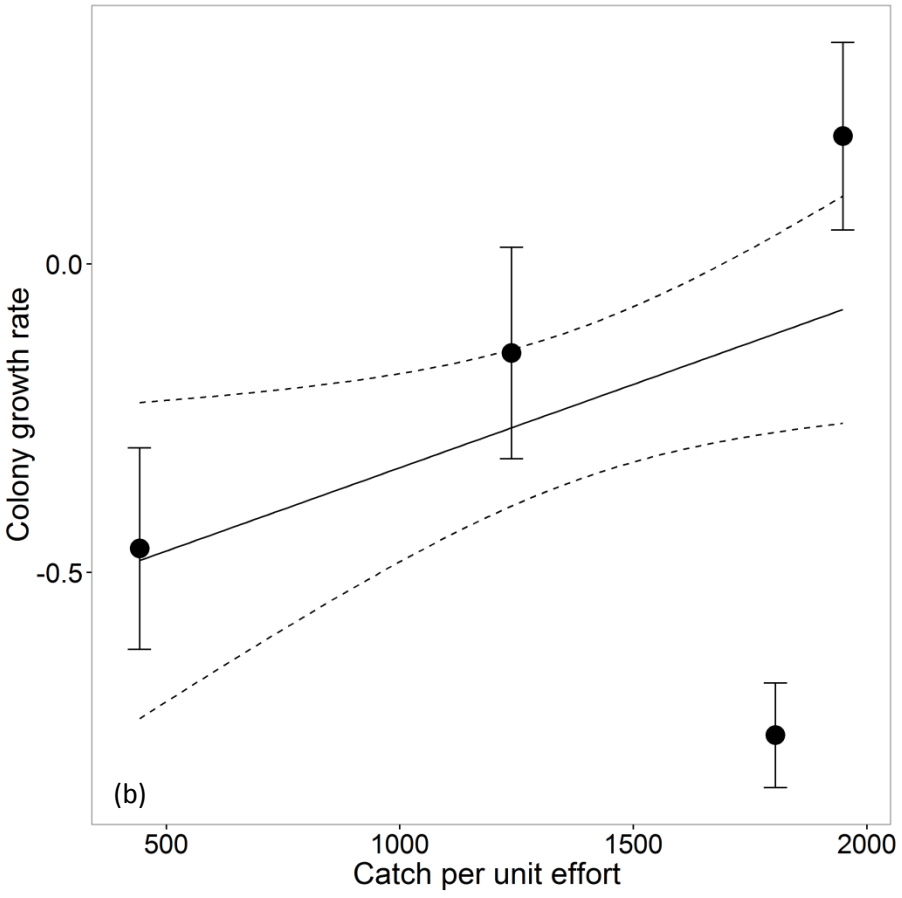

N
Southern Hebrides
45 South Minch
47 Northern Ireland
46 Cyde
Solway Firth
50 Irish Sea
0 75 150 300 Kilometers

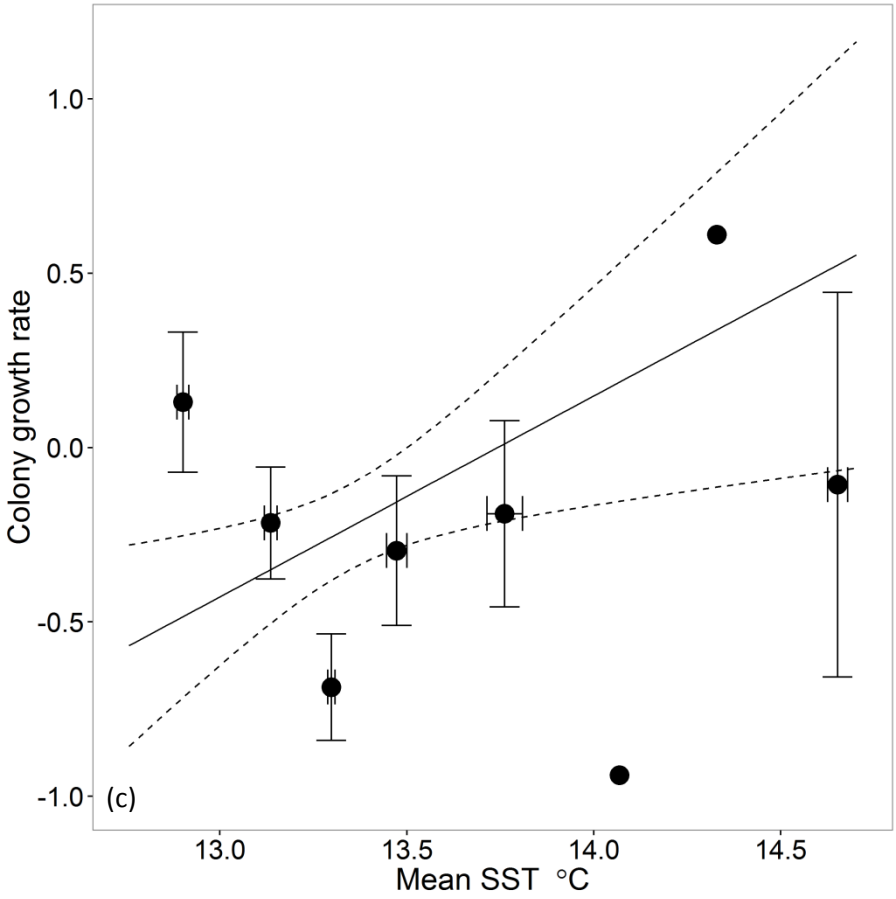

N
Colony Size
1 - 13
14 - 37
38 - 81
Clusters
0.42 - 0.99
-0.50 - 0.20
-0.67 - -1.00
(a)
0 25 50 100 km

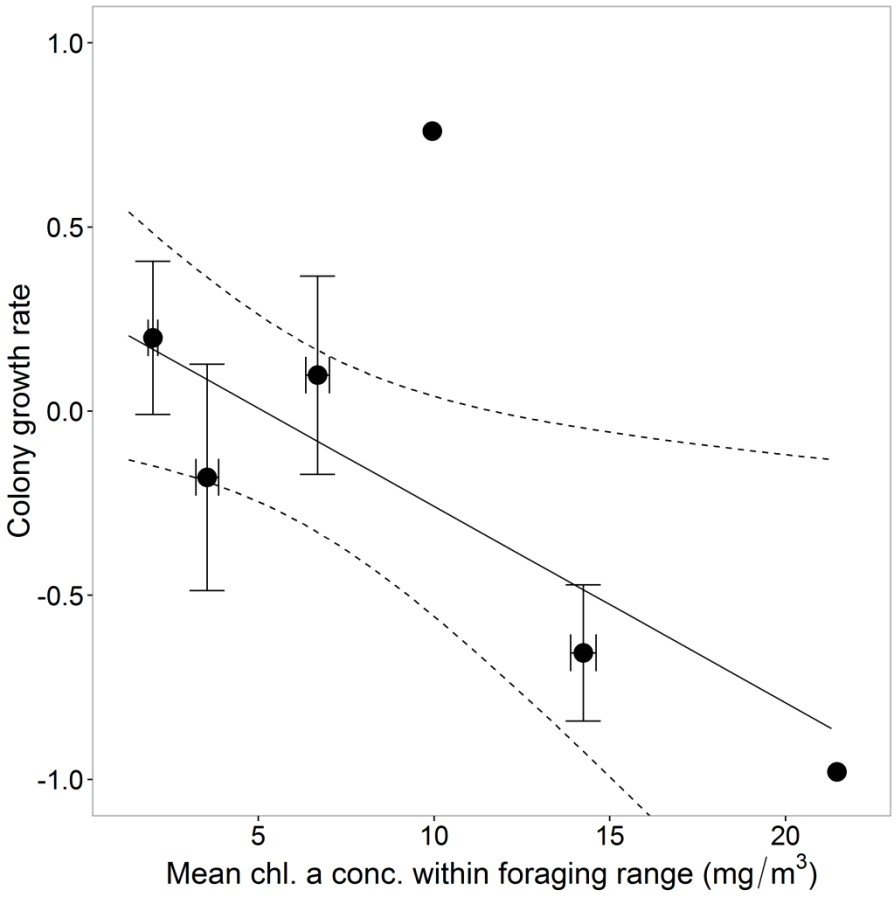

N
Colony Size
2 - 100
101 - 300
301 - 692
693 - 1810
1811 - 4830
Clusters
0.86 - 1.00
-0.10 - 0.69
-0.27 - -0.55
-0.69 - -1.00
(b)
0 25 50 100 km


N
Colony Size
1 - 50
51 - 150
151 - 300
301 - 1500
Clusters
0.80 - 0.99
0.25 - 0.70
-0.72 - - 1.00
(c)
0 25 50 100 km


0.5
0.0
-0.5
-1.0
Colony growth rate
(a)
400
800
1200
1600
Wave fetch (km)


0.0
-0.5
Colony growth rate
(b)
500
1000
1500
2000
Catch per unit effort


1.0
0.5
0.0
-0.5
-1.0
Colony growth rate
(c)
13.0
13.5
14.0
14.5
Mean SST °C


1.0
0.5
0.0
-0.5
-1.0
Colony growth rate
5
10
15
20
Mean chl. a conc. within foraging range (mg/m3)